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## COLLECTION OF MAMMAL MANURE AND OTHER DEBRIS BY NESTING BURROWING OWLS

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**ABSTRACT.**—Burrowing Owls (*Athene cunicularia*) routinely collect and scatter dry manure of mammals around their nesting burrows. Recent studies have suggested this behavior attracts insect prey to the nesting burrow. However, some Burrowing Owls do not use manure, but instead, collect and scatter other materials (e.g., grass, moss, paper, plastic) around their nesting burrow in a similar fashion. Use of these materials seemingly contradicts the prey-attraction hypothesis. Using observational and experimental methods, we tested whether Burrowing Owls preferred manure to other materials commonly found at nesting burrows in eastern Washington. We found a wide variety of materials at nests, but grass and manure were the most common materials. The amount of manure present at nests was negatively correlated with the amount of other materials, and with the distance to the nearest source of manure. Burrowing Owls showed no preference between horse manure and grass divots at experimental supply stations that we placed near nesting burrows. They did prefer these two materials to carpet pieces and aluminum foil (both materials that are often found at Burrowing Owl nests). Our results did not support the premise that Burrowing Owls specifically seek out manure when lining their nesting burrows. The unusual behavior of collecting and scattering mammal manure and other debris at Burrowing Owl nests may serve functions other than (or in addition to) prey attraction and alternative hypotheses need further testing before the function of this behavior is certain.

**KEY WORDS:** Burrowing Owl; *Athene cunicularia*; dung; manure; nesting behavior; tool use.

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### COLECCIÓN DE ESTIÉRCOL DE MAMÍFEROS Y OTROS RESIDUOS POR INDIVIDUOS DE *ATHENE CUNICULARIA* QUE SE ENCUENTRAN ANIDANDO

**RESUMEN.**—El búho *Athene cunicularia* recolecta y dispersa de forma rutinaria estiércol seco de mamíferos alrededor de sus madrigueras de anidación. Estudios recientes han sugerido que este comportamiento atrae a sus presas (insectos) a la madriguera de anidación. Sin embargo, algunos búhos no utilizan estiércol sino que dispersan y recolectan de una manera similar otros materiales (e.g., hierba, musgo, papel, plástico) alrededor de sus madrigueras de anidación. El uso de estos materiales aparentemente contradice la hipótesis de la presa de atracción. Utilizando métodos de observación y experimentales, probamos si *Athene cunicularia* prefiere estiércol ante otros materiales comúnmente encontrados en sus madrigueras de anidación. Encontramos una gran variedad de materiales en los nidos, pero la hierba y el estiércol fueron los materiales más comunes. La cantidad de estiércol presente en los nidos se correlacionó negativamente con la cantidad de otros materiales, y con la distancia a la fuente más cercana de estiércol. Los búhos no mostraron preferencia diferenciada entre estiércol de caballo y hierba en las estaciones de suministro experimental que fueron colocadas cerca de las madrigueras de anidación. Sin embargo, presentaron una mayor preferencia por estos dos materiales que por pedazos de alfombra y papel de aluminio (ambos materiales se encuentran a menudo en los nidos de *A. cunicularia*). Nuestros resultados no apoyan la premisa de que los búhos *A. cunicularia* buscan específicamente estiércol para colocar material alrededor de sus madrigueras de anidación. El comportamiento inusual de *A. cunicularia* de recolectar y dispersar estiércol de mamíferos y otros restos alrededor de sus nidos puede desempeñar otras funciones fuera de (o además de) la atracción de presas por lo que es necesario probar otras hipótesis alternativas antes de establecer la función cierta de este comportamiento.

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Animals often collect nonfood materials from the environment to incorporate into nests, or to scatter around their nest entrance or mating site. While seemingly peculiar, such behaviors have been shown to serve useful functions. Perhaps the most well-known example is male bowerbirds (family Ptilonorhynchidae) that collect bright, colorful objects to attract mates (Borgia 1985a). However, collection of non-food materials serves a host of other functions in a diverse array of taxa including birds, mammals, and insects. Organic materials such as lichen flakes, carnivore scat, and cactus segments can reduce nest depredation by acting as visual camouflage (Hansell 1996, 2000), olfactory camouflage (Schuetz 2005), or by physically deterring predators (Brown et al. 1972). Inorganic materials such as stones and charcoal deposited around nest entrances can aid thermoregulation by narrowing temperature fluctuations of eggs (Yosef and Afik 1999) or by increasing nest temperature (Smith and Tschinkel 2007). Plant materials such as volatile compounds and solidified resin can provide anti-parasite (Clark 1991) or antimicrobial properties (Christe et al. 2003). A variety of objects are sometimes used as signals of territorial advertisements (Bergo 1987, Selas 1988) or colony recognition (Grasso et al. 2005). However, the function of these behaviors was not always obvious prior to research focused specifically on these behaviors.

Another peculiar use of non-food material is the collection of mammal manure by birds (Boehm 1991) including some raptors (e.g., *Buteo regalis*; Bowles and Decker 1931) and ground-nesting birds (e.g., *Geococcyx californianus*; Hughes 1996). Numerous hypotheses have been proposed to explain the function of mammal manure at bird nests, but few studies have tested predictions of the various functional hypotheses. One exception is the unusual pattern of manure collection by Burrowing Owls (*Athene cunicularia*). Burrowing Owls are well known for their unusual behavior of collecting and depositing dried manure of mammals (usually from horses and cows) at their nest burrows (Fig. 1). This behavior has been reported for over a century (Bendire 1892, Scott 1940), but is not known to occur in other species of owls in the genus *Athene*. Most species that incorporate mammal manure into their nest appear to use the manure as nest-lining material, but Burrowing Owls greatly exaggerate this behavior. Throughout their breeding range, Burrowing Owls shred large clumps of dried manure to build their underground nest cup, to place

in the tunnel leading to the nest chamber, and to scatter around the entrance to their nesting burrow (Bendire 1892, Scott 1940, Martin 1973, Green and Anthony 1989).

Until recently, the use of mammal manure was widely believed to reduce nest depredation by camouflaging the scent of Burrowing Owl nests from potential predators (Martin 1973; Green 1983, 1988; Green and Anthony 1989; Green et al. 1993; Haug et al. 1993; Desmond et al. 1997; Green and Anthony 1997; Griebel 2000; Dechant et al. 2003; Holmes et al. 2003). However, this hypothesis had never been tested experimentally and alternative hypotheses were never considered.

Three key approaches that have helped to differentiate among alternative mechanistic hypotheses and clarify the function of collecting nonfood materials in other taxa are to: (1) identify the types of materials that are most preferred in experimental trials (Borgia et al. 1987, Borgia and Keagy 2006), (2) ensure that the prevailing hypothesis adequately explains all important features of the behavior (Borgia 1985b), and (3) remove or supplement the material at nest or display sites and record the consequences to the bird (Borgia 1985a, Borgia and Presgraves 1998). Several recent studies of Burrowing Owls utilized approach number (3) above (experimental manipulations of manure) and failed to find support for the antipredator hypothesis (Brady 2004, Levey et al. 2004, Smith 2004, Smith and Conway 2007). Instead, experimental results supported a new hypothesis: that Burrowing Owls collect manure to attract arthropod prey to their burrow (Levey et al. 2004, Smith 2004, Smith and Conway 2007). However, no previous studies have used the first two approaches listed above to evaluate alternative hypotheses for this unusual behavior. For example, one pattern that seems to contradict the prey-attraction hypothesis is that Burrowing Owls commonly collect and scatter other materials (e.g., grass, moss, paper, plastic, aluminum foil, carpet) in the same way they do with manure (Thomsen 1971, Smith 2004). The use of other materials has been observed throughout the breeding range of Burrowing Owls. Smith and Conway (2007) reported that of 45 occupied nesting burrows studied in 2002 in south-central Washington, 21 had manure present and 100% of these with manure also had other debris present; but the other 24 had only debris present (no manure). Like manure, these other materials are quickly replaced if removed; and they first increase, then decrease in abundance during

the course of the nesting cycle (M. Smith and C. Conway unpubl. data). Despite the frequency with which other debris (other than manure) is used by Burrowing Owls, its function has not been experimentally addressed by previous studies that have focused exclusively on the use of manure. Neither the prey-attraction hypothesis nor the olfactory-camouflage hypothesis can easily explain the use of these other materials. Do Burrowing Owls collect other materials for the same reason(s) they collect manure, or do owls collect manure and these other materials for different reasons?

A first step in evaluating why Burrowing Owls collect and deposit nonfood materials at their nest is to determine if they have a preference for what materials they collect (approach number [1] listed above). The prey-attraction hypothesis predicts that owls will prefer manure to other materials. If owls show no preference for manure in experimental trials, this would suggest either: (1) owls collect various materials (including manure) for some reason(s) other than prey attraction, (2) collecting manure serves one function and collecting other materials serves another function, or (3) the other materials collected by owls also attract prey. To better understand the function of manure-collection behavior in Burrowing Owls, we used both experimental and observational approaches to examine whether manure is a sought-after and preferred material compared to other debris commonly found at Burrowing Owl nests.

#### METHODS

We conducted research from February to September 2000–02 in south-central Washington, U.S.A. The ~520-km<sup>2</sup> study site in Franklin and Benton counties is 109–150 m above sea level near the towns of Richland, Kennewick, and Pasco, Washington. Annual precipitation averages 18 cm, primarily as rain from November to February (Hoitink and Burk 1995, Benton Clean Air Authority 2004). Land use in these counties includes urban, suburban, industrial, agricultural, and horse- and cattle-grazing interspersed with some native shrub-steppe. Burrowing Owls nested in many of the above land-use categories, but nests used for this study were predominantly located in industrial areas with little human presence and where the native shrub-steppe had been moderately disturbed (Smith 2004).

We located Burrowing Owl nests via standardized roadside surveys (Conway and Simon 2003), incidentally during daily field activities, and by asking

landowners where they had seen owls (as part of a larger demographic study; Conway et al. 2006). From the 45 occupied nesting burrows on our study site in 2002, we randomly selected 20 that were known to be in the incubation stage (because males have begun depositing materials at nests at this stage).

**Cataloging Materials.** From 19 April–3 May 2002, we visited each of the 20 nesting burrows twice (separated by at least 1 wk) and gathered all material from a 1-m radius surrounding the nest entrance and within the first 0.5 m of the nest tunnel. Materials from the two visits to each nest were combined, and all materials were then dried, sorted, and grouped into seven categories: (1) grass, (2) other organic matter (e.g., moss, root clumps), (3) horse or cow manure, (4) canid scat (i.e., dog, coyote), (5) other species' manure (e.g., marmot, goose), (6) shredded paper and plastic, and (7) other human-made products (e.g., leather glove, rope). For each nesting burrow, we recorded the total mass (g) of each type of material, and also visually estimated the proportion (by volume) of materials in each of the seven categories. We used this second approach (proportional volume) to account for the fact that the total amount of material present varied among nests. We used repeated-measures ANOVAs to compare the abundance of the seven types of material found at the 20 natural nesting burrows. The within-subjects factor (i.e., the repeated measure) was the mass of each material in the first ANOVA, and the proportional volume of each material in the second ANOVA. We then conducted Bonferroni pair-wise comparisons to identify specific differences. We also used a Spearman rank correlation to examine the relationships between the proportions of materials found at the 20 natural nesting burrows.

**Distance to Source of Materials.** The relationship between the amount of manure present at a nesting burrow and the distance to the nearest source of manure can provide information about whether Burrowing Owls prefer manure to other materials. If Burrowing Owls prefer to deposit mammal manure at their nests, we expected manure use to be consistently high regardless of how far the nearest source was (i.e., no correlation between amount of manure and distance to source of manure), at least up until some threshold distance. Beyond this distance (at which collection would be too costly), the amount of manure present at a burrow would likely decline rapidly. In contrast, if owls simply use the most convenient and readily available materials,

then the amount of manure present at a nest should decline more steadily (i.e., exponential or linear decrease) as distance to the nearest source of manure increased. We located the nearest source of manure by searching the area around each of the 20 nesting burrows on foot (300 m radius) and by vehicle (up to 800 m radius). We then measured the distance with a measuring wheel. Potential sources of manure were both active or inactive livestock areas that ranged from open (unfenced) areas that were clearly used by livestock (small livestock paths and trails were apparent) to large fenced pastures. Manure, if present, was easy for human observers to detect in the vicinity of nesting burrows, and ranged in moisture level from moist to old and caked-dry. Inspections of nesting burrows in Washington, Arizona (M. Smith unpubl. data), and Florida (D. Levey pers. comm.), and videotape recordings of manure collection in Canada (D. Todd and R. Poulin pers. comm.) show that owls most often collect moderately-dry manure, and do not collect fresh, wet manure. We used simple linear regressions to determine whether the amount of manure present at a nesting burrow (by mass and proportional volume) was related to the distance to the nearest source of manure.

**Supply Stations.** In 2001 and 2002, we presented a distinct subset (i.e., we excluded burrows where we collected deposited materials) of Burrowing Owls with various materials to more directly evaluate the extent to which they preferred to use manure relative to other materials often found at nesting burrows. We placed "supply stations" at 16 randomly chosen nesting burrows (2001:  $n = 10$ ; 2002:  $n = 6$ ) that were not used for any other experiments. Each supply station contained 2 liters of each of four types of material (masses correspond to 2 liters): 5- $\times$ -5 cm white carpet pieces (260 g), 13- $\times$ -8 cm fresh grass divots from a golf course (330 g), moderately dry (but with some moisture remaining) and shredded (3- $\times$ -3 cm) horse manure (510 g), and 2-cm pieces of compacted aluminum foil (70 g). We chose these materials because they were commonly found at Burrowing Owl nests on our study site. The amount of manure and grass divots that we placed at each supply station was similar to what is naturally found at nests, but the amount of carpet and aluminum foil was much greater than typically observed at nests. We chose to use more carpet and aluminum foil than is naturally found because we wanted to offer owls the same amount of each material so as to not influence their choice (and to offer more manure and grass than is naturally found would have

made the supply stations prohibitively large). To construct a supply station, we taped together four cardboard beverage flats (46  $\times$  30 cm each) and placed a different material in each of the four sections. The four materials were placed haphazardly in the four sections at each supply station. From 1-15 April (just prior to the laying and incubation stages when owls typically begin collecting material), we placed supply stations 10 m away from the entrance of each nesting burrow at a random azimuth. We visited each nesting burrow once every 5 d until 31 July (mean number of visits at each burrow =  $14.3 \pm 0.7$  SE). If  $\geq 50\%$  of a material appeared to be missing from a supply station, we weighed the remaining material in the supply station, and refilled each section so that the original amount (2 liters) was available again. We had to replenish materials infrequently (in 2001 for example: only 20% of nests had manure replaced once, 30% of nests had divots replaced once, 10% had divots replaced twice, 10% had divots replaced three times, and 10% had divots replaced five times). After each nest check, we discarded all materials from the nest entrance and the first 0.5 m of the nesting burrow. We were unable to distinguish manure and grass that owls collected from our supply stations from that which they collected from the surrounding landscape. However, we marked our manure and grass divots with ultraviolet powder, and subsequently found marked materials from the supply stations at nesting burrows, demonstrating that owls were responsible (at least partially) for the materials missing from our supply stations. Additionally, we have little reason to expect that materials would have been removed by other animals, or would be blown away (the supply stations had sides that prevented displacement).

We calculated the total mass of each material ( $M$ ) that was used from each supply station with the formula

$$M = \sum_{n=1}^k b - r_m \quad (1)$$

where  $b$  was the mass of the material at the beginning of the experiment (and was also the final mass of each material after we refilled it);  $r_m$  is the mass of material remaining on visit  $n$ ; and  $k$  is the total number of refill-visits. From these values we estimated the total volume ( $V$ ) of each material used, and the volume remaining on each visit ( $r_v$ )

$$V = \frac{M}{\lambda} \quad (2)$$

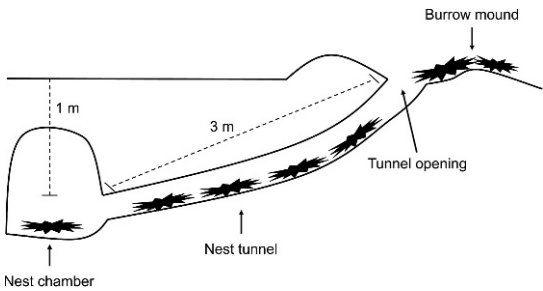


Figure 1. Throughout their breeding range, Burrowing Owls deposit nonfood material (e.g., dried manure, grass, paper) at their nesting burrows. Although the use of such materials occurs in other bird species, Burrowing Owls exaggerate this behavior by scattering materials in their underground nest chamber, in the tunnel leading to the nest chamber, and around the entrance to their nesting burrow.

$$r_v = \frac{r_m}{\lambda} \tag{3}$$

where  $\lambda$  is the mass of 1 liter of material. The total volume of each material supplied over the course of the study ( $S$ ) depended on the number of visits during which we added new material, and the amount of material remaining on that visit.

$$S = \sum_{n=1}^k (2 - r_v) + 2 \tag{4}$$

Using these equations, we then calculated the percent volume of supplied material used by owls.

$$\text{Percent used} = \frac{V}{S} (100) \tag{5}$$

We used repeated-measures ANOVAs to test for differences in the amount of the four materials that were removed from our supply stations. The within-subjects factor (i.e., the repeated measure) was the volume of each material in the first ANOVA, and the percent of the supplied material used (by volume) in the second ANOVA. We then conducted Bonferroni pair-wise comparisons to identify specific differences among the four types of materials.

To meet the assumptions of normality and homogeneity of variance, we log-transformed all masses and distances, and arc-sine square-root transformed all proportions (including percent of supplied material used). We considered differences statistically significant if  $P < 0.05$ . Analyses were performed using JMP 8.0 (SAS Institute Inc.) and SPSS 18.0 (IBM Corp.), and figures were made in SigmaPlot 11.0 (Systat Software Inc.).

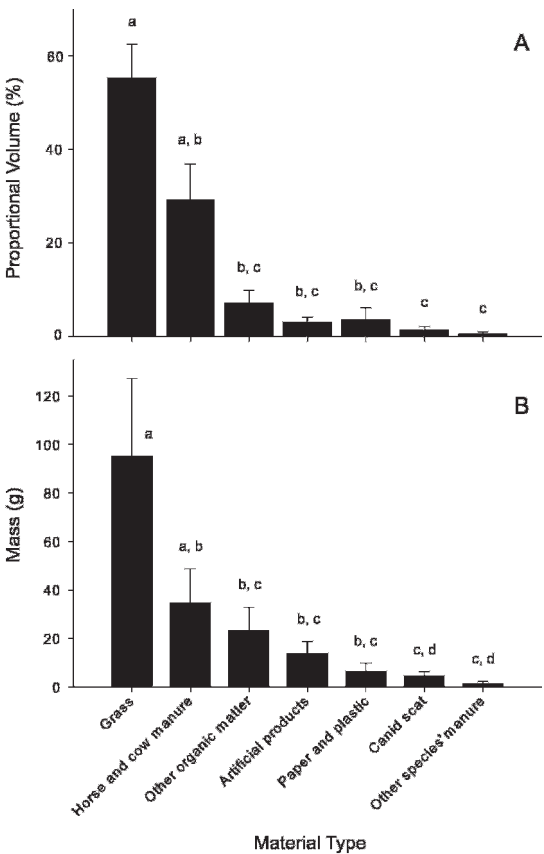


Figure 2. Mean proportional volume (A) and mass (B)  $\pm$ SE of organic and human-made materials found at Burrowing Owl nesting burrows ( $n = 20$ ) from two nest visits during April to May 2002 in south-central Washington. Bars that share a common letter were not different based on repeated measures ANOVA, Bonferroni pair-wise comparisons for: (A) proportional volume relative to other materials present, and (B) mass (g).

RESULTS

We found a variety of different materials at the entrances to the subset of 20 nests that did not receive supply stations (Table 1, Fig. 2). We found differences among the seven materials in both the mass ( $F_{6,114} = 12.6, P < 0.001$ ) and the proportion ( $F_{6,114} = 20.9, P < 0.001$ ) present at nests. Grass and manure were more common at nest burrows than all other materials; and canid scat, paper and plastic, and other species' manure were the least commonly found materials (Table 1, Fig. 2).

We found a negative correlation between the proportion (arc-sine square-root transformed) of manure present at nests and the proportion (arc-sine



Table 1. Back-transformed mean difference and SE (lower bound, upper bound) and significance for Bonferroni pairwise comparisons of materials found at Burrowing Owl nests (natural variation), and materials removed from supply stations in south-central Washington, U.S.A.

| MATERIALS SOURCE                     |                                       | COMPARISON      | MEAN DIFFERENCE | SE (LOWER) | SE (UPPER) | P-VALUE |
|--------------------------------------|---------------------------------------|-----------------|-----------------|------------|------------|---------|
| Natural variation:<br>mass (g)       | Grass > other organic matter          | 93              | 37              | 236        | 0.002      |         |
|                                      | Grass > canid scat                    | 895             | 331             | 2421       | 0.001      |         |
|                                      | Grass > artificial products           | 153             | 57              | 409        | 0.001      |         |
|                                      | Grass > paper and plastic             | 552             | 261             | 1167       | 0.001      |         |
|                                      | Grass > other species manure          | 2723            | 1200            | 6310       | 0.001      |         |
|                                      | Horse manure > canid scat             | 44              | 16              | 121        | 0.029      |         |
|                                      | Horse manure > other spp. manure      | 134             | 51              | 348        | 0.001      |         |
| Natural variation:<br>proportion (%) | Grass > canid scat                    | 51              | 41              | 61         | 0.001      |         |
|                                      | Grass > artificial products           | 45              | 34              | 55         | 0.001      |         |
|                                      | Grass > paper and plastic             | 47              | 37              | 57         | 0.001      |         |
|                                      | Grass > other species manure          | 55              | 46              | 64         | 0.001      |         |
|                                      | Horse manure > canid scat             | 18              | 10              | 27         | 0.017      |         |
|                                      | Horse manure > other spp. manure      | 20              | 12              | 30         | 0.009      |         |
|                                      | Supply station:<br>volume removed (l) | Divots > carpet | 2.8             | 2.4        | 3.2        | 0.001   |
| Divots > aluminum                    |                                       | 2.6             | 2.2             | 3.0        | 0.001      |         |
| Manure > carpet                      |                                       | 2.3             | 2.1             | 2.4        | 0.001      |         |
| Manure > aluminum foil               |                                       | 2.1             | 2.0             | 2.3        | 0.001      |         |
| Supply station:<br>percent removed   | Divots > carpet                       | 51              | 44              | 58         | 0.001      |         |
|                                      | Divots > aluminum foil                | 61              | 52              | 70         | 0.001      |         |
|                                      | Manure > carpet                       | 26              | 22              | 30         | 0.001      |         |
|                                      | Manure > aluminum foil                | 63              | 53              | 72         | 0.001      |         |

square-root transformed) of many of the other materials present at nests: grass (Spearman's  $P = -0.79$ ,  $P < 0.001$ ), paper and plastic (Spearman's  $P = -0.63$ ,  $P = 0.003$ ), and other organic materials (Spearman's  $P = -0.41$ ,  $P = 0.076$ ). The amount of manure at a nest was negatively correlated with the distance from the nearest source of manure for both mass of manure present ( $r^2 = 0.20$ ,  $F_{1,18} = 4.5$ ,  $P = 0.047$ ,  $n = 20$ ) and proportional volume of manure relative to other materials ( $r^2 = 0.31$ ,  $F_{1,18} = 8.2$ ,  $P = 0.01$ ,  $n = 20$ ; Fig. 3). However, the relationship between manure mass and distance to source was highly influenced by a single data point; we failed to find a statistically significant relationship between manure mass and distance to source when this point was removed ( $r^2 = 0.11$ ,  $F_{1,17} = 2.0$ ,  $P = 0.174$ ;  $n = 19$ ). In contrast, the relationship between proportional volume of manure and distance to source remained statistically significant when we removed this data point ( $r^2 = 0.25$ ,  $F_{1,17} = 5.7$ ,  $P = 0.029$ ,  $n = 19$ ).

Burrowing Owls did not use all four materials from our supply stations equally and the results were similar for both volume ( $F_{3,45} = 43.8$ ,  $P < 0.001$ ) and percent ( $F_{3,45} = 78.5$ ,  $P < 0.001$ ) of supplied materials used. The volume of grass and manure used by

Burrowing Owls did not differ, but both were used more commonly than carpet or aluminum foil (which did not differ from each other; Fig. 4).

DISCUSSION

In our study area, Burrowing Owls primarily collected grass and mammal manure (horse and cow) to scatter in and around their nesting burrows. The dung of other species and debris such as shredded paper, plastic, and cardboard were also used, but much less commonly. We found similar results at our supply stations; Burrowing Owls did not show a preference between horse manure and grass divots, but preferred both of these materials to carpet and aluminum foil. The amount of manure present at nesting burrows was negatively correlated with the amounts of other materials, and more weakly correlated with the distance to the nearest source of manure. Moreover, several owls nesting very close to sources of manure used a great deal of grass, but little (or no) manure. Taken together, these results indicate that Burrowing Owls use the most readily available materials, rather than showing a strong preference for manure when lining their nesting burrows.

The frequent use of other materials (one Burrowing Owl in our study even shredded and scattered

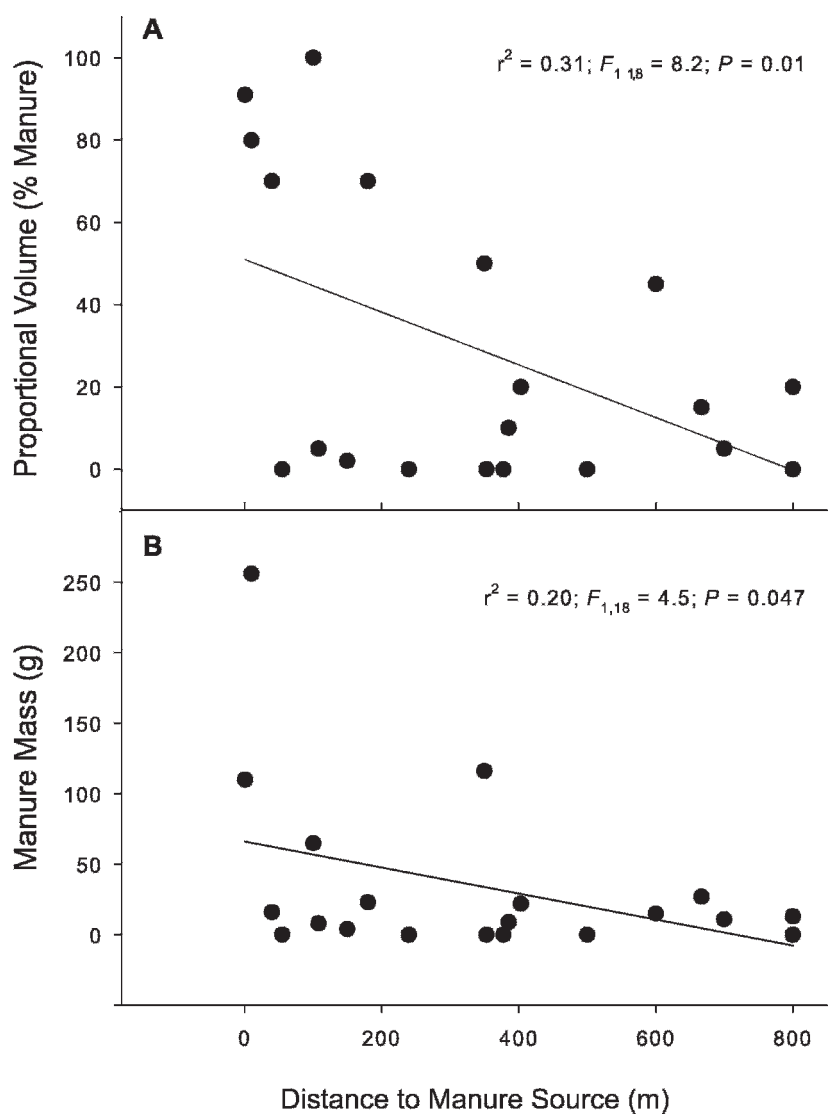


Figure 3. The relationship between (A) percent, and (B) mass of horse and cow manure present at Burrowing Owl nesting burrows ( $n = 20$ ), and the distance to the nearest source of manure (e.g., horse pasture) in south-central Washington in 2002.

the cardboard supply station) and an apparent lack of a clear preference for manure suggests one of three possibilities: (1) that prey attraction may not be the primary function of manure-collection behavior in Burrowing Owls, and may have evolved as part of a broader behavioral repertoire, the function of which remains unknown, (2) Burrowing Owls collect manure to attract prey but collect other materials for some other reason, or (3) the other materials that Burrowing Owls collect and scatter

around their burrows also function to attract prey. We believe that Burrowing Owls most likely collect and scatter manure and other debris for the same reason (i.e., we think the second possibility above is unlikely) because some owls seem to use debris in the same manner as other owls use manure (i.e., the seasonal timing, amount, and location are all similar and they seemed to be used in place of each other at different nests). The negative correlations between the amount of manure and the amount of other



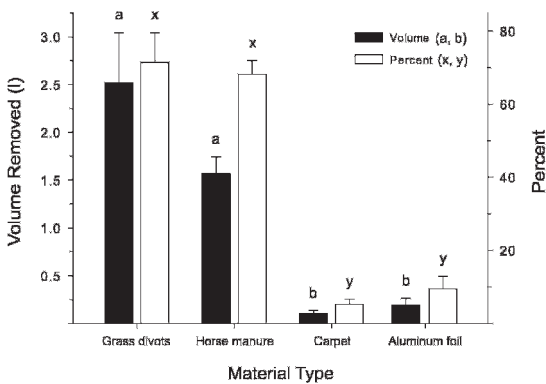


Figure 4. Mean volume and percent of supplied material by volume  $\pm$ SE (horse manure, grass divots, carpet, and aluminum foil) that was removed from supply stations placed 10 m away from Burrowing Owl nests ( $n = 16$ ) in 2001 and 2002 in south-central Washington. Bars that share a common letter (a, b for volume; x, y for percent of supplied) were not different based on repeated-measures ANOVA, Bonferroni pair-wise comparisons.

materials also appear to support this conclusion. However, individual behaviors of animals sometimes have more than one function (Borgia 1995), and a myriad of alternative hypotheses have been proposed for the use of manure in nests (see Green and Anthony 1989, Boehm 1991, Griebel 2000, Brady 2004, Levey et al. 2004, Smith and Conway 2007). Future studies need to consider the possibility that different materials collected by Burrowing Owls serve different functions. One hypothesis that has received some support is that all of these unusual materials signal conspecifics that a burrow is occupied, thus reducing agonistic interactions (Smith and Conway 2007). This hypothesis warrants further study.

However, the most parsimonious hypothesis to explain the function of manure collection would also explain the fact that owls often use other materials in place of manure. If manure collection functions to attract insects, then it is puzzling that some owls nesting very close to horse pastures lined their nests with only grass and not manure. Such findings would appear to contradict the conclusions of past studies that support the prey-attraction hypothesis (Levey et al. 2004, Smith and Conway 2007). However, the mechanism(s) by which manure attracts insects to Burrowing Owl nests has not been examined; grass and other materials commonly used by Burrowing Owls might also attract insects. Piles of material such as grass, moss, paper, and cardboard may trap moisture and provide microhabitat (e.g., for egg-laying) for

many species of insects. Future studies might productively examine the extent to which the other materials used by Burrowing Owls attract insects (and if so, how) throughout the breeding range of Burrowing Owls. Additionally, quantifying the effect of the presence of manure on juvenile survival and other factors related to fitness is necessary. We believe that until such studies are completed, the mystery as to why Burrowing Owls collect and scatter mammal manure and other debris around their nesting burrows remains unresolved.

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